Phenetics and Ecology of Hybridization in Buckeye Butterflies (Lepidoptera: Nymphalidae).
Hafernik, J. E., Jr. University of California Publications in Entomology, Volume 96, pp. 109. 1982.

In his great book *How to Become Extinct*, the late, lamented humorist Will Cuppy wrote: "The term *species*, in its application to fish, was first clearly defined by F. Willughby in his *Historia Piscium* (1686), and from that day to this the whole thing has been in a fearful muddle." Although Buckeyes are not fish, they might as well be; at least they are in a fearful muddle. There is enough in that muddle to generate at least ten Ph.D. theses. This is the first of them.

Hafernik defines his objectives in the Introduction. It is characteristic of scientific writing that work is always presented as rigorously logical, completely planned in a rational manner in advance—despite the serendipitous character of so much research, the blunders and false starts and lucky breaks we all know well. Thus, it appears from his own words that Hafernik was immensely successful at meeting his objectives. He was, in fact, reasonably successful in his attempt to apply the biological species concept to most (not all) of the North and Middle American *Junonia*. He did not, however, settle definitively the row begun by W. T. M. Forbes 55 years ago as to whether the Buckeyes represent a case of "circular overlap." That is a pity, because the concept is a classic challenge to the biological species definition, and there are very few good cases around. (*Pieris napi* and *bryoniae* in Europe *may* be one of them.)

The study entailed making many hybrid crosses and carrying them to the F_2 and backcrosses in order to quantify Oliver's compatibility parameters. Making crosses in Buckeyes is not like making crosses in Pierids. These animals do not mate readily in cages and cannot be hand-paired, and one has to use experienced wild males subjected to a bait-and-switch technique using chilled virgins. The technique is tedious; having used it myself I can say I would rather go to the dentist. The resulting adults were used as reference groups for discriminant-function analysis, for the analysis of the inheritance of phenotypic differences between taxa, and for field tests of the visual component of reproductive isolation. Discriminant analysis is a powerful tool in systematics and particularly in analyzing intergrading populations (cf. the forthcoming volume by M. M. Collins on *Hyalophora*, Saturniidae, in the same U.C. series), but its power is inherently limited by the insight of the investigator in selecting character systems and reference populations. In itself, it is powerless to distinguish between primary intergradation and the secondary kind, that is, hybridization. John Endler has argued on theoretical grounds that this distinction is *generally* very difficult or impossible. Hafernik does not really address this question, nor does he provide any historical scenario to account for the present distribution of the entities in *Junonia*. For the super-rigorous Popperians, failure to tell tales is praiseworthy; for those of us brought up on them, it is a let-down.

Hafernik arrives at twelve conclusions. They are a mixed lot, some on much firmer footing than others. Here they are, with comments.

1. "Phenotypic differences in color among North and Central American *Junonia* are probably not associated with major genomic reorganization, but are rather the result of allelic differences at a few loci." This is based on the remarkably high levels of genetic and developmental compatibility among the entities. It seems plain now

that reproductive isolation can occur based on changes in a minuscule portion of the genome (Hawaiian *Drosophila*) and that organisms which are phenotypically very different can be astonishingly similar genomically (man and the chimpanzee), so Hafernik's finding (not, by the way, including any biochemical genetics) is not all that surprising.

2. "Color pattern differences among females act as isolating mechanisms, with males courting females with color patterns similar to their own." O.K. as far as it goes. Unfortunately, no workable assay was found to quantitate *female* preference among *males* (we have seen that this is a very important component in *Colias* hybridization, for example), so only half the story has been told. (See also Shapiro, 1983, *Psyche* 90:59-65 for an experiment which corroborates Hafernik's conclusions while eliminating a potential methodological problem.)

3. "Pheromones may not be important for *Junonia* courtship. Males can recognize prospective mates by color pattern and flight pattern alone." Perhaps, but the potential role of pheromones has not been rigorously *excluded*.

4. "Reproductive isolation can arise from changes at one or a few loci controlling color patterns." When 1, 2 and 3 above are combined as premises in a classic syllogism, this is the logical conclusion.

5. "Although unlike phenotypes are courted infrequently, males are less discriminating in their choice of a mate during the late stages of courtship. This condition leads to hybridization." Perhaps; certainly plausible.

6. "Hybridization is largely restricted to areas where at least one species is common, and thus there are many opportunities for mistaken courtships." Better quantification of density-relatedness is desirable; it has proved to be a major factor in the *Colias* hybridization story.

7. "F_1 and backcrosses are highly fertile, and this may result in introgression. In South Texas, genes of *J. coenia* have apparently been incorporated into the gene pool of *J. nigrosuffusa*." Independent evidence, such as *might* be provided by electrophoresis, is desirable here; it might also help to test the inference that we are seeing secondary, not primary, intergradation.

8. "Individuals of *Junonia* are quite vagile and range widely. . .movements of individuals into areas of sympatry. . .from areas of allopatry probably retard selection for perfection of isolating mechanisms." No surprise here. The surprise is that the eminently logical model for reinforcement of reproductive isolating mechanisms in secondary sympatry, long a staple in our evolutionary diet, is now under attack and seems to stand on pitifully little *evidence*.

9. "Incomplete reproductive isolation may be a recent result of man's activities, which have produced large new habitats, more contiguous ranges, and larger population sizes." Could be (I argue the same way about the hybridizing Pierids of the genus *Tatochila* in NW Patagonia!), but as usual, the documentation for such claims is, well, nonexistent.

10. "Phenetic studies show. . .typical *J. zonalis* and *J. nigrosuffusa*. . .should be considered conspecific and combined under *J. evarete*. *J. coenia* is a species that is broadly sympatric with and at least partially reproductively isolated from *J. evarete*." By Hafernik's own statement, isolation between *nigrosuffusa* and *coenia* is nearly complete in southeastern Arizona, perhaps incomplete in Florida, and demonstrably incomplete in Texas. The Caribbean remains a black box. In short, we know a lot more than Forbes did, and yet it still seems that *coenia* and *evarete* are "almost" species, more so in some places than others. That is the price we pay for

believing that speciation is a *process*.

11. "*Junonia coenia* and *J. nigrosuffusa* have different oviposition and larval foodpant preferences in Texas." Unequivocally true; "habitat selection" might have been added, too.

12. "Larval foodplant preferences. . .in areas of sympatry are probably related to the effects of both competition and hybridization." Well, maybe, but as usual, references to competition in phytophagous insects are basically baloney: there is little evidence that it even *exists*, let alone being a major organizing force in communities.

So much for the first chapter in the unraveling of the Buckeye problem. Before summing up, let me—as a member of the Editorial Board of U.C. Publications in Entomology—put in a good word for "house organs." Far too many theses or other studies which form unified wholes are chopped up more or less arbitrarily to generate journal articles. *U.C. Pubs. in Ent.* offers an important outlet for work which should be kept together and which transcends the length limits of most journals. It is particularly attractive for biosystematic work. Its past record includes such classic revisionary work as MacNeill's on *Hesperia* and Burns' on *Erynnis*. Alas, the physical format of recent volumes is not so attractive as in the "old days," but efforts are being made to change that. Contributions to the U.C. series are refereed, both in- and out-of-house.

The Buckeyes are still a fearful muddle. Who out there is ready to take on the Caribbean basin populations?

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Butterflies East of the Great Plains: An Illustrated Natural History.
Opler, Paul A. and George O. Krizek, 1984. Johns Hopkins University Press, Baltimore and London. 294 pp. Price: $49.50.

This is *not* a field guide. In fact, it is not certain what it *is*, but whatever it is, it is outstanding.

Butterflies East of the Great Plains is a medium-large format book, 8 ¾" x 11 ¼", about the size of many college textbooks. Although there is no way it can fit in a pocket, it is in many ways the logical successor to A. B. Klots' *Field Guide to the Butterflies of North America, East of the Great Plains*. It covers the same well-worked yet constantly surprising fauna (but for the U.S. only). The introduction, by Jerry Powell, gives Klots the credit he so richly deserves for making the living butterfly the focus of our attention; it is thus somewhat annoying to see the jacket blurb praise the present book as "like no other. . .the first butterfly book ever to emphasize the butterfly as a living organism rather than a specimen." At any rate, the book is in a lineal tradition from William Henry Edwards and Samuel Hubbard Scudder through Alexander Barrett Klots, and that in itself is a strong recommendation.

Opler and Krizek do *update* Klots, incorporating a great deal of information accumulated since 1951 on biology, behavior, and especially host-plant relations and geographic distribution. These are not referenced as a rule—this is a popular, not a scholarly, treatise—but they are presented with some care, so that the